

Stabilization of new carbon inputs rather than old carbon decomposition determines soil organic carbon shifts following woody or herbaceous vegetation transitions

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Abstract

Background and aims Although numerous studies have quantified the effects of land-use changes on soil organic carbon (SOC) stocks, few have examined simultaneously the weight of carbon (C) inputs vs. outputs in shaping these changes. We quantified the relative importance of soil C inputs and outputs in determining SOC changes following the conversion of natural ecosystems to pastures or tree plantations, and evaluated them in light of variations in biomass production, its quality (C:N) and above/belowground allocation patterns.

Methods We sampled soils up to one-meter depth under native grasslands or forests and compared them to adjacent sites with pastures or plantations to estimate the proportion of new SOC (SOC_{new}) retained in the soil and the decomposition rates of old SOC ($k_{SOC-old}$) based on $\delta^{13}C$ shifts. We also analyzed these changes in the particulate organic matter fraction (POM) and estimated above and belowground net primary production (ANPP and BNPP) from satellite images, as well as changes in vegetation and soil's C:N ratios.

Results The conversion of grasslands to tree plantations decreased total SOC contents while the conversion of forests to pastures increased SOC contents in the topsoil but decreased them in deep layers, maintaining similar soil stocks up to 1 m. Changes in POM were less important and occurred only in the topsoil after cultivating pastures, following SOC changes. Surprisingly, both land-use trajectories showed similar decomposition rates in the topsoil and therefore overall SOC changes were not correlated with C outputs ($k_{SOC-old}$) but were significantly correlated with C inputs and their stabilization as SOC_{new} (similar results were obtained for the POM fraction). Pastures although decreased ANPP (as compared to forest) they increased belowground allocation and C:N ratios of their inputs to the soil, probably favoring the retention and stabilization of their new C inputs. In contrast, tree plantations increased ANPP but decreased BNPP (as compared to grasslands) and scarcely accumulated SOC_{new} probably as a result of the high C retention in standing biomass.

Conclusions Our results suggest that SOC changes are mainly controlled by the quantity and quality of C inputs

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and their retention in the soil, rather than by C outputs in these perennial subtropical ecosystems.

Keywords Soil organic carbon · Decomposition rate · Roots · Lands use change

Introduction

Vegetation changes can alter soil organic carbon (SOC) stocks substantially, potentially increasing carbon (C) emissions to the atmosphere. Several studies have shown that the replacement of native vegetation by annual crops reduces SOC stocks (Lal 2004; Post and Mann 1990). However, the effects of cultivation on SOC are less clear after replacing native vegetation with perennial species, including pastures and tree plantations (Desjardins et al. 2004; Lisboa et al. 2009; Mosquera et al. 2012; Neill et al. 1997; Powers and Veldkamp 2005; Chen et al. 2004; Epron et al. 2009; Guo et al. 2008; Zinn et al. 2002). In a previous study we analyzed changes in SOC stocks after replacing different native vegetation types with plantations or pastures (Eclesia et al. 2012). Our regional meta-analysis and field research showed that changes in SOC stocks were relatively independent of the initial vegetation type (native forests and grasslands) and more dependent on the final one (cultivated pastures and tree plantations), with pastures showing relatively greater and more consistent increases in SOC than plantations. Here we examine the underlying mechanisms causing these patterns of SOC change by quantifying the relative role of C inputs and its stabilization as new SOC, relative to C outputs promoted by decomposition of old SOC, through their imprint on soil $\delta^{13}\text{C}$.

Although numerous studies have quantified the effects of land use changes on SOC stocks (Batlle-Bayer et al. 2010; Guo and Gifford 2002; Jackson et al. 2002; Post and Kwon 2000), few have examined the relative weight that the associated alterations of C inputs and outputs had dictating stock shifts. Since changes in SOC stocks arise from an altered balance between C inputs and outputs through time (Amundson 2001), increases can arise from either decreased SOC outputs, increased SOC inputs, or both (Epstein et al. 2002; Post and Kwon 2000). Similarly, decreases could arise from an increase in C outputs and/or a decrease in C inputs. In addition, by analyzing the isolated response of C inputs and C outputs to land use changes, interactions with environmental factors such as fertility or water availability can be more easily uncovered (Berthrong et al. 2012; Eclesia et al. 2012; Song et al.

2012). By observing actual process such as net primary production, heterotrophic respiration, and decomposition; rather than their integrated effect on net SOC shifts, a better understanding of their rates and controls can emerge (Raich and Tufekcioglu 2000; Trumbore 1997).

Carbon inputs to the soil can be altered by changing net primary production (NPP) and its proportional allocation to the belowground or aboveground domain (BNPP and ANPP, respectively). Soil C inputs can be approximated by subtracting NPP from the biomass accumulated in standing vegetation and consumed by herbivores, as NPP sets the maximum amount of C that may enter the soil (Jenkinson et al. 1999). Carbon retention in biomass compartments can be important in ecosystems that face rapid accrual, such as young tree plantations, in which relatively high NPP does not translate immediately to high biomass inputs to the soil (Eclesia et al. 2012). In addition, the ratio of BNPP:ANPP strongly affects C inputs to the soil and is determined by environmental factors, but more importantly by plant functional types (Bolinder et al. 2007). Generally, the relative proportion of NPP allocated belowground is higher in ecosystems dominated by herbaceous vs. woody and perennial vs. annual plants (Lauenroth and Gill 2003; Zhou and Luo 2008). This allocation is also higher in cooler climates (Hui and Jackson 2006; Ruimy et al. 1994). Therefore, changes in plant traits after land use changes may alter the ratio of BNPP:ANPP and, in consequence, C inputs to the soil and SOC formation, even when NPP may remain unchanged (Guo et al. 2007).

Carbon outputs from SOC stocks are determined by decomposition rates, influenced by abiotic factors such as precipitation, temperature, and soil texture and biotic factors including the plant attributes (e.g., tissue quality) and the community of decomposers (Cotrufo et al. 2013; Kemmitt et al. 2008; Schimel and Schaeffer 2012). Soil organic C outputs usually increase with higher mean annual precipitation and temperature and decrease in finer soil textures (Amundson 2001; Hopkins et al. 2012). Land use and vegetation changes may alter SOC decomposition by changing abiotic factors such as microclimate conditions (i.e. promoting changes in soil temperature or moisture)(Batlle-Aguilar et al. 2011). In addition, vegetation may potentially increase decomposition rates by increasing the supply of nutrients and energy to decomposers through “priming” (Fontaine et al. 2003; Kuzyakov 2010; Mazzilli et al. 2014). The quality of plant inputs (particularly its C:N ratio) can also affect the retention and stabilization of SOC in more recalcitrant SOC pools (Mazzilli et al. 2014; Kuzyakov 2010).

Altered SOC stocks caused by land use change may affect soil organic matter (SOM) fractions differently (Bernoux et al. 1998; Davidson and Janssens 2006; Giardina and Ryan 2000; Paul et al. 1999). Labile fractions of SOM typically have higher C:N ratios similar to plant residues, while more stabilized fractions have lower C:N ratios, narrower variations and longer mean residence times (Cambardella and Elliott 1992; Golchin et al. 1994a, b). Labile fractions also tend to have higher decomposition rates (k) and to be more sensitive to land-use changes in the short-term (Christensen 1996). However, recent studies have shown that land use changes may also modify the most stabilized SOC fractions, even in relatively short time periods and in deep layers (Hopkins et al. 2012; Piñeiro et al. 2009). Richards et al. (2007) compared pastures and pine plantations and observed that C inputs to the light SOM fraction were similar under both land uses, but C inputs to stable SOC fractions were lower in pine plantations than in pastures and their native predecessor. Thus, there is strong evidence that land use changes may affect both newer and older organic matter fractions, but there is no consensus on which effect is stronger or its variations in depth.

When vegetation shifts involve the replacement of C_3 by C_4 species or vice versa, the proportion of SOC that derives from the old and the new vegetation type can be determined using ^{13}C stable isotope analyses. Since C_3 and C_4 species have very different isotopic signatures (C_3 plants have $\delta^{13}\text{C} \approx -26 \text{‰}$ and C_4 have $\delta^{13}\text{C} \approx -12 \text{‰}$), the SOM formed from each group of species will resemble the composition of their biomass. Mixing models are typically used to isolate these contributions (Balesdent and Mariotti 1987) and several studies have used stable isotopes to estimate k values and mean residence time ($\text{MRT} = 1/k$) of SOM pools (Amundson and Baisden 2001; Balesdent and Mariotti 1987; Bernoux et al. 1998; Koutika et al. 1997; Paul et al. 2008). The combination of ^{13}C isotopes analyses with SOM fractionation can also lead to new insights on the effects of land use transitions on C dynamics of different soil fractions (Lisboa et al. 2009).

Understanding the relative importance of C inputs or outputs to the soil driving net SOC changes can inform about management practices that maximize soil carbon sequestration. Currently, most of the management strategies implemented to increase SOC attempt to reduce C outputs, usually by reducing plowing or the occurrence of fires after land use clearing. These practices have

contributed to reduced erosion, increased aggregate stability, and reduced C losses through decomposition. However, C inputs may also be managed to increase SOC stocks (Kong et al. 2005), although they are more commonly ignored. Determining the relative importance of C inputs and outputs for SOC formation is critical to anticipate the success of these two management strategies.

The objectives of this study were: (1) to quantify the relative weight of C inputs and outputs determining SOC changes in different soil fractions after the conversion of natural ecosystems to pastures or plantations; and (2) to estimate the associated changes in net primary productivity (NPP), quality (C/N ratios), and allocation (above/belowground productivity) between the systems. To achieve these objectives, we sampled paired stands of native vegetation and pastures or plantations up to one-meter depth and estimated the proportion of new SOC and SOC decomposition rates using changes in $\delta^{13}\text{C}$. We also estimated above and belowground net primary production (ANPP and BNPP) of each site using satellite images.

Materials and methods

Study sites and experimental design

The study was carried out in northeastern Argentina (27°S , 54°W) at sites in the provinces of Misiones and Corrientes (Fig. 1). The region has a rolling landscape with average slopes lower than 5 % and deep lateritic soils classified as Ultisols and Alfisols (Ligier et al. 1988). The climate is humid subtropical and lacks a pronounced dry season. Mean precipitation is 1600 mm in the south and 2000 mm in the north of the study region, while mean annual temperature is 20°C and similar across all the study region (Ligier et al. 1988).

The region offers a diverse set of native and cultivated vegetation types and land-use trajectories for both woody and herbaceous vegetation. In this study, six sites were sampled, in our analyses (Table 1 and Fig. 1) as they showed significant changes in ^{13}C SOC ratios to be useful for our isotopic analyses, as explained below. At each site, we selected a stand of natural vegetation adjacent to a stand with cultivated vegetation (at all sites natural vegetation were replaced only once and by the current land use), using the natural vegetation to provide

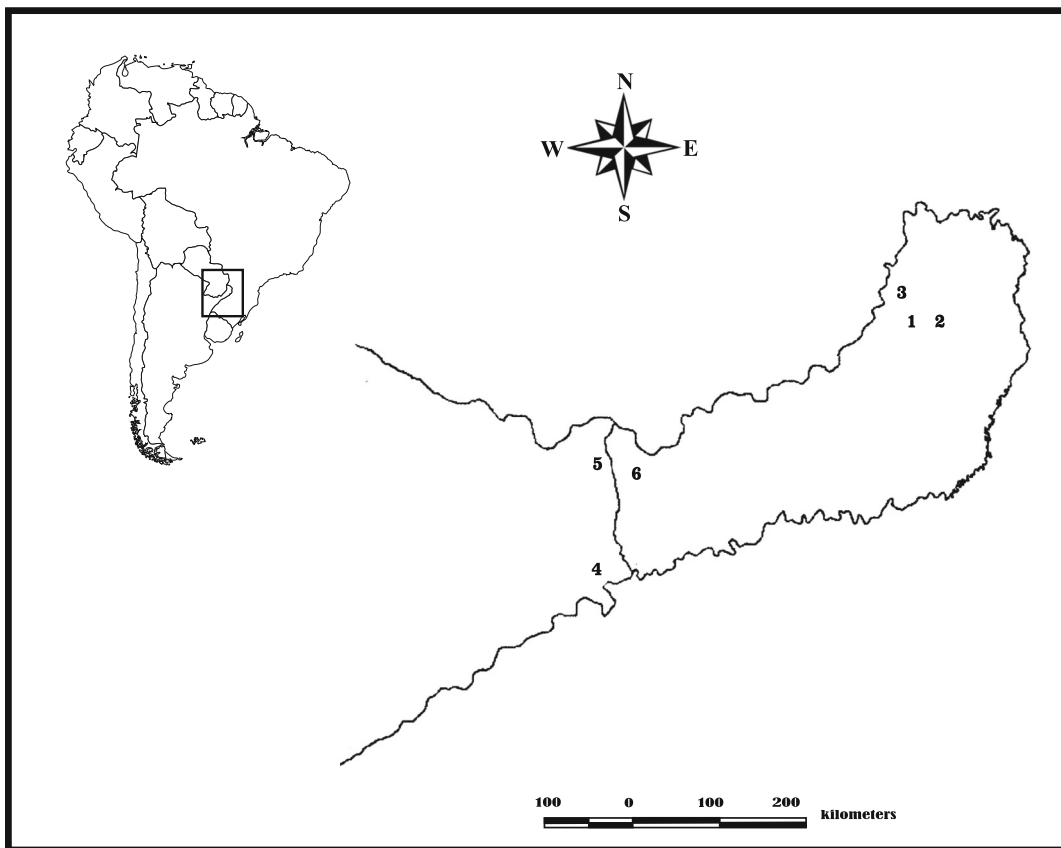


Fig. 1 Map showing the location of our study sites. In the northern portion of Misiones province, sites 1, 2 and 3 represent native forest to pasture transitions and in the southern part of the study region, sites 4, 5 and 6 are grasslands converted to tree plantations

initial characteristics for the adjacent stand before cultivation. We evaluated three stands with tree plantations

that were established over grasslands and three pasture stands that were established over natural forests. These

Table 1 Characteristics of the study sites

Site	N°	Lat-Long	Departament-Province	Land use	Age (years)	Clay + silt content (%)
Robicué II	1	26° 05'07.6" S 54° 24' 52.6" W	Iguazú (Misiones)	Forest Pasture	65	98 94
Robicué I	2	26° 05'07.6" S 54° 24' 52.6" W	Iguazú (Misiones)	Forest Pasture	25	98 93
E ^o . Vilm	3	26° 00' 28.4" S 54°30'40.7" WO	Iguazú (Misiones)	Forest Pasture	55	95 93
La Península	4	28°17'11.4" S 55°50'54.6" WO	Santo Tomé (Corrientes)	Grassland Plantation	15	92 93
Santo Tomás	5	27°35'44.8" S 55°57'25.4" WO	Ituzaingó (Corrientes)	Grassland Plantation	31	95 95
Santa Cecilia	6	27°28'14.9" S 55°41'13.1" WO	Candelaria (Misiones)	Grassland Plantation	25	89 89

changes cover two land-use trajectories in the region from native vegetation: grassland to tree plantation (G-T) and forest to pasture (F-P). All F-P transitions had a strong change from C₃ to C₄ vegetation altering ¹³C SOC values, while all G-T transitions had a strong change from C₄ to C₃ vegetation affecting ¹³C SOC contents (see Figs. 2 and 3). Detailed descriptions of native ecosystems can be found elsewhere (Carnovali 1994; Erize et al. 1997; Parodi 1964; Soriano et al. 1992). The tree plantations studied here included pine species, including *Pinus elliotti* and *Pinus taeda*, and the cultivated pastures were dominated by *Axonopus compressus* or *Brachiaria brizantha* (Table 1). Pastures and grasslands were grazed by cattle with stocking rates of ~0.7 cows ha⁻¹. Selected pastures and tree plantation sites had different ages since their establishment over the native ecosystems generating a cronosequence (see Table 1).

Field sampling and lab analyses

Soil, roots and litter samples were taken from adjacent native and cultivated stands, at least 30 m away from their boundary to avoid possible edge effects. The top 100 cm of soil were sampled using a 2-cm-wide soil corer, with 4 to 6 subsamples pooled in each stand. Samples were separated into 0–5, 5–10, 10–20, 20–30, 30–50, 50–70 and 70–100 cm depth intervals. All samples were passed through a 2-mm sieve and were oven-dried at 60 °C to constant weight. Soil organic matter fractions were determined according to Cambardella and Elliott (1992). Briefly, 10 g of 2-mm-sieved soil were shaken overnight (18 h) in 30 ml 5 % hexametaphosphate dispersant solution. The dispersed soil was then sieved with a 53 μm-mesh sieve and washed several times with distilled water. The material left on the sieve constituted the sand fraction, from

Fig. 2 SOC and C-POM stocks (a–c) and its ¹³C isotopic values (b–d) under grasslands (*open circles*) and tree plantations (*black triangles*) at different soil depths. *Open circles* and *black triangles* in **b** and **d** panels not connected with lines indicate ¹³C isotopic values of litter (*top*) and fine roots (*bottom*), for grasslands and tree plantations, respectively

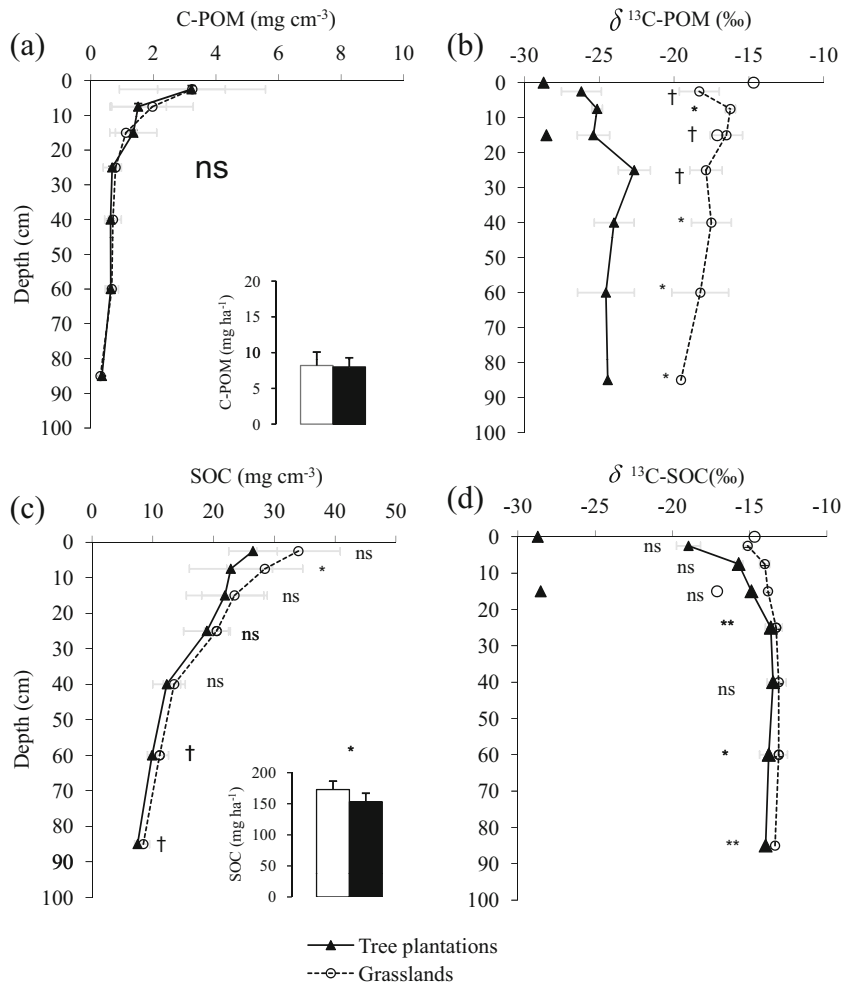
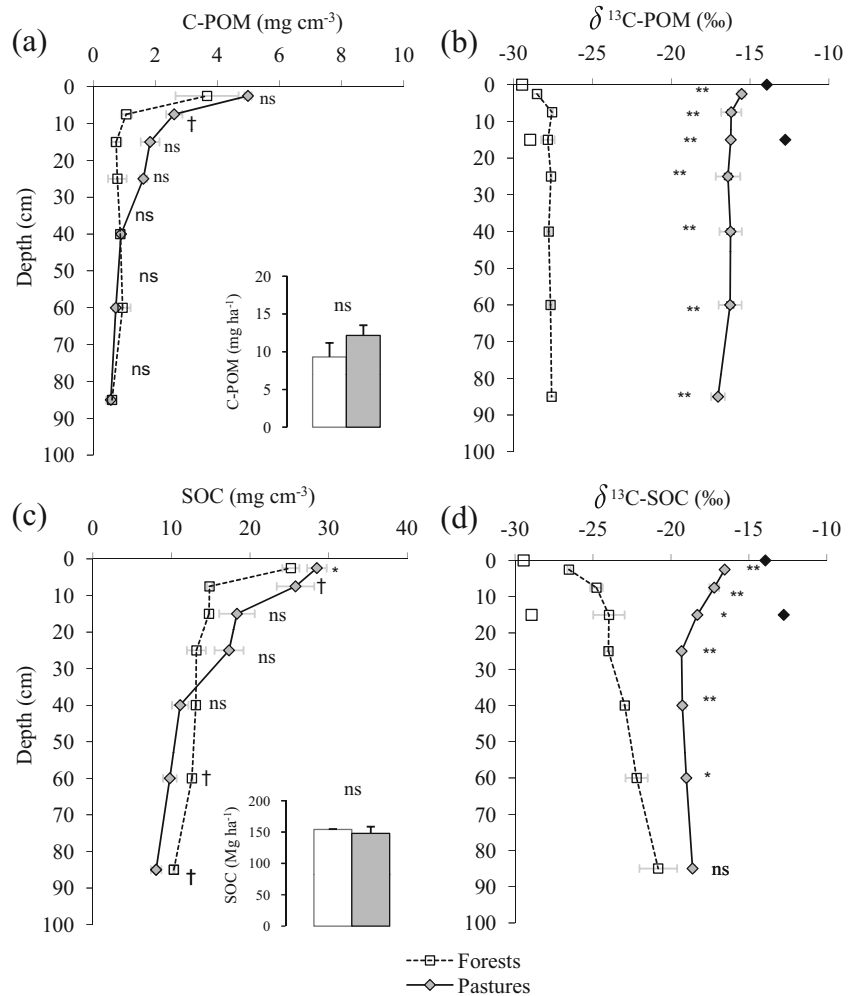


Fig. 3 SOC and C-POM stocks (a–c) and its $\delta^{13}\text{C}$ isotopic values (b–d) under forest (*open squares*) and pasture (*grey diamonds*) at different soil depths. *Open squares* and *grey diamonds* in b and d panels not connected with lines indicate $\delta^{13}\text{C}$ isotopic values of litter (*top*) and fine roots (*bottom*), for forest and pastures, respectively



which the particulate organic matter (C-POM) was measured, and the material that went through the sieve constituted the clay + silt fraction, termed the mineral associated organic matter (MAOM). Both fractions were collected separately and oven dried at 60 °C until they reached a constant mass. The samples of the clay + silt fraction were ground with a mill (IKA, Model M20), whereas the sand fraction was ground to dust with a manual mortar. C and N concentrations and natural abundance of SOM ^{13}C were determined with an elemental analyzer (Carlo Erba) coupled to a mass spectrometer (Finnigan MAT) in the Stable Isotope Laboratory at Duke University, USA. Together with the soil C samples, four subsamples were taken from each depth interval to estimate bulk density (BD) using 6-cm cylinders. Soil resemblance between adjacent stands –and therefore the space by time substitution

assumption – was evaluated based on soil texture (Table 1), and differences in clay + silt contents were observed to be always less than 5 %. Soils were tested for the presence of carbonates with negative results.

Fine roots were sampled at random locations in tree plantations and forests to a depth of 30 cm. Coarse and fine roots were separated by hand in the laboratory and only root diameters <5 mm were included in our analyses, to estimate only the rapidly cycling component of the belowground system, commonly associated with SOC formation. In grasslands and pastures root samples were taken using a 7-cm-wide soil core down to 30 cm depth (three subsamples per stand). In all stands three litter subsamples were taken using a 25.5-cm-wide ring. Roots and litter were separated from the soil by hand and oven-dried at 60 °C for 24 h, then homogenized and ground to fine powder for chemical analysis. C and N

concentrations and ^{13}C content in roots and litter were analyzed by dry combustion in a elemental analyzer (Carlo Erba) coupled to a mass spectrometer (Finnigan MAT) in the isotope lab at Duke University.

Estimates of soil organic C contents

Soil organic C contents in each fraction and depth were corrected to an equivalent soil mass to avoid overestimates of carbon stocks in any potentially compacted sites (Davidson and Ackerman 1993; Henderson 1995). The SOC contents (Mg ha^{-1}) for each soil fraction were estimated using the following equation:

$$\text{SOC} = \frac{\text{Wf} \cdot \text{CP} \cdot \text{BD} \cdot \text{Z} \cdot 100}{\text{Ws}} \quad (1)$$

Where Wf is the weight (g) of fraction (POM or MAOM), CP is the percentage of C for each fraction, BD is bulk density (Mg m^{-3}), Z is corrected depth (m) and Ws is total soil weight prior to fractionation (g) (Solomon et al. 2002; Sollins et al. 1999). To isolate any soil compaction effects, the sampling depth in cultivated systems (pasture or tree plantations) were corrected using the following equation:

$$Z = \left(\frac{\text{BDn}}{\text{DBp}} \right) \cdot X \quad (2)$$

where, BDp is bulk density (Mg m^{-3}) of soils in the cultivated (i.e., planted) systems, BDn is bulk density (Mg m^{-3}) of soils in natural grassland or forest systems, and X is the soil sampling depth (m) (Solomon et al. 2002).

Estimates of C inputs to the soil and decomposition rates

SOC stocks derived from the native vegetation and those derived from the new cultivated vegetation were estimated for the POM fraction and for total SOC (POM + MAOM). No estimates were obtained for the pure MAOM fraction because the isotopic signature for C inputs to this fraction is unknown. We define “new SOC” as the total C contributed by the new cultivated vegetation that entered the soil after establishment and “old SOC” as the carbon contributed by the native vegetation prior to vegetation replacement.

To estimate the SOC (and C-POM) derived from new vegetation, we used the following equations (Balesdent and Mariotti 1996):

$$\text{fSOC}_{\text{new}}(\%) = ((\delta - \delta_o) / (\delta_v - \delta_o)) \times 100 \quad (3)$$

Where fSOC_{new} is the fraction of SOC derived from the new vegetation (tree plantations or pastures) (in %) that is present in the soil under the new land use; δ is the $\delta^{13}\text{C}$ value of the SOC after the replacement of native vegetation by tree plantations or pastures; δ_o is the $\delta^{13}\text{C}$ value of the SOC under the original native vegetation and δ_v is the $\delta^{13}\text{C}$ value of the C inputs to the soil (litter plus roots) derived from new vegetation. We used the average ^{13}C value of roots and litter to set δ_v , but we made a sensitivity analysis using root and litter ^{13}C separately and fSOC_{new} values varied less than 4.2 % on average (no significant differences at $p > 0.1$), therefore not affecting our results.

Finally, to convert the fSOC_{new} in percent to SOC_{new} in stocks (Mg ha^{-1}), we used the following equation:

$$\text{SOC}_{\text{new}} = (\text{fSOC}_{\text{new}} \times \text{SOC}_e) / 100 \quad (4)$$

where SOC_e is the final SOC stock measured under the new land use. SOC_{new} represents the amount of C that entered the soil and remained there during the experimental period and constitutes a minimum estimate of soil C inputs.

To estimate the amount of old SOC (and C-POM) derived from the native vegetation that remained under the new vegetation (SOC_{old}), we used the following equation:

$$\text{SOC}_{\text{old}} = \text{SOC}_e - \text{SOC}_{\text{new}} \quad (5)$$

We also estimated the fraction of the original SOC derived from the native vegetation that is still remaining under the new vegetation at the sampling time ($\text{fSOC}_{\text{old-remaining}}$ - an analogous term to the fraction of biomass remaining through time in litter decomposition studies) with the formula:

$$\text{fSOC}_{\text{old-remaining}} = \text{SOC}_{\text{old}} / \text{SOC}_i \quad (6)$$

where C_i is the initial or original SOC stock obtained from samples taken under the native vegetation.

The decomposition rate (k) of the total SOC and the POM fraction were estimated using a negative first order exponential model (Dalal and Mayer 1986):

$$\text{SOC}_{\text{old}} = \text{SOC}_i e^{-k_{\text{SOC-old}} \cdot t} \quad (7)$$

$$k_{\text{SOC-old}} = -(\ln f\text{SOC}_{\text{old-remaining}})/t \quad (8)$$

where $k_{\text{SOC-old}}$ is the average SOC decomposition rate of the old SOC that occurred after the replacement of the native vegetation by pastures or tree plantations. As stated initially, all of these calculations were performed for the entire SOC and for the POM fraction alone, therefore obtaining C-POM_{new} and $k_{\text{POM-old}}$ values using $\delta^{13}\text{C}$ and C contents measured in the POM fraction (see all abbreviations in Appendix Table 4).

Estimates of net primary production with remote sensing data

Aboveground net primary production (ANPP) of each ecosystem was estimated using satellite images, following the model of Monteith (1972) in which ANPP is obtained by multiplying the amount of photosynthetically active radiation absorbed by vegetation (APAR) by the energy conversion efficiency (ϵ). APAR depends on the incident photosynthetically active radiation (PAR) and on the fraction of PAR absorbed by green vegetation (fPAR). PAR was calculated using incident radiation obtained from meteorological stations located at Posadas and Iguazú (Misiones province). PAR was estimated as 48 % of the incident radiation (McCree 1972) and fPAR was derived from the normalized difference vegetation index (NDVI) obtained from satellite images capture by the MODIS sensor. The NDVI was calculated using bands 1 (red, 620–670 nm) and 2 (infrared, 842–856 nm). We used the MOD13Q1 product with a spatial resolution (pixel) of 5.33 ha and a temporal resolution of 16 days (<ftp://e4ftl01u.ocs.nasa.gov/MOLT/MOD13Q1.005/>), accumulating 23 images per year. We extracted MODIS pixels for all stands assuring that they were completely included in a single vegetation type, covering the area where soil samples were taken. Mean NDVI was calculated for each stand and for each date of the MODIS series. fPAR was estimated as a linear function of NDVI, assigning zero absorption to the NDVI value corresponding to pixels without vegetation cover and the maximum absorption value (fPAR = 0.95) to plots in the area with the highest

vegetation cover (Piñeiro et al. 2006). The resulting equation was: fPAR = min (1.3914*NDVI-0.2863; 0.95). Epsilon (ϵ) values for the different vegetation types were obtained from the literature as described in Table 2 (Malhi et al. 2009; Ruimy et al. 1994; Turner et al. 2006). Belowground net primary production (BNPP) of each ecosystem was estimated using previously reported BNPP/ANPP ratios (Parelo et al. 2010; Ruimy et al. 1994; Yadvinder et al. 2009). The BNPP/ANPP ratios used were: 0.33 for forests, 0.29 for tree plantations and 1.1 for both pastures and grasslands.

Statistical analysis

To compare the changes in C stocks (SOC and C-POM) and fluxes (SOC_{new}, $k_{\text{SOC-old}}$, C-POM_{new}, $k_{\text{POM-old}}$) that occurred after cultivation with pastures ($n = 3$) or tree plantations ($n = 3$) we used ANOVA and considered each paired site as a block. Because all sites differed in the time elapsed since conversion, changes in SOC and C-POM stocks or SOC_{new} and C-POM_{new} were compared at annual rates to correct for different lengths periods. We also performed simple regression analyses to determine the relationship between SOC_{new}, $k_{\text{SOC-old}}$, C-POM_{new}, $k_{\text{POM-old}}$ against observed changes in SOC or C-POM contents. All data was tested for normality (Shapiro-Wilk test), and regressions were considered significant at $p < 0.05$. Net primary production (aboveground, belowground and total NPP) and biomass C:N ratios of the vegetation (pastures, forests, grasslands and plantations) were compared using ANOVA, again using sites as blocks. Significant differences were indicated with standard statistical nomenclature (** = $p < 0.01$; * = $p < 0.05$ and † = $p < 0.1$).

Results

The conversion of grasslands to tree plantations decreased total SOC contents while the conversion of forests to pastures increased SOC contents in the surface soil but decreased it in deep layers, maintaining similar soil stocks up to 1 m (Figs. 2 and 3). Tree plantations lost on average 19 Mg ha⁻¹ of SOC ($p < 0.01$) in the first meter of the soil, although changes layer by layer were significant only in three of the seven depths studied (Fig. 2c). Significant increases in SOC stocks were observed in the first 10 cm of the soil profile after planting pastures and significant decreases in the deeper soil layers (>60 cm).

Table 2 Net, below and aboveground production of forests converted to pastures and grasslands converted to tree plantations as estimated from NDVI of MODIS satellites

Site	Ecosystems ^a	Initial land use			Current land use			Differences		
		ANPP	BNPP	NPP	ANPP	BNPP	NPP	ANPP	BNPP	NPP
1	F-P	19.50	6.44	25.90	14.30	15.70	30.10	-5.15	9.34	4.18
2	F-P	19.50	6.44	25.90	14.20	15.60	29.80	-5.28	9.20	3.91
3	F-P	18.80	6.20	24.90	13.60	15.00	28.60	-5.13	8.81	3.67
4	G-T	7.83	8.61	16.40	20.80	6.07	26.90	13.10	-2.54	10.50
5	G-T	7.87	8.66	16.50	23.40	6.79	30.10	15.50	-1.87	13.60
6	G-T	7.44	8.18	15.60	18.60	5.41	24.00	11.20	-2.77	8.39
Means comparing the new land use										
Pastures								-5.19*a	9.12*a	3.92*b
Plantation								13.27*b	-2.39*b	10.83*a

Different letters within a column indicate significant differences $p < 0.05$ between pastures and plantations and the asterisk indicate a significant change after conversion to pasture or to tree plantation at $p < 0.05$

NPP net primary productivity, *ANPP* aboveground net primary productivity, *BNPP* belowground net primary productivity. All are expressed in Mg of biomass ha⁻¹ year⁻¹

^a *F* forest, *G* grassland, *P* pasture, *T* tree plantation

Changes in C-POM stocks were less important in magnitude and increases occurred in the first 20 cm of soil only after planting pastures, while no differences were observed in the whole profile for either pastures or tree plantations (Figs. 2 and 3). Tree plantations decreased overall $\delta^{13}\text{C}$ values of SOC and C-POM for all layers analyzed (on average from -13.7 to -14.9 for SOC and from -17.7 to -24.6 for the C-POM fraction), although some layers showed no significant trends (Fig. 2). On the other hand, pastures showed large increases in $\delta^{13}\text{C}$ values of SOC and C-POM for all layers analyzed (on average from -23.6 to -18.6 for SOC and from -27.7 to -16.2 for the C-POM fraction) (Fig. 3).

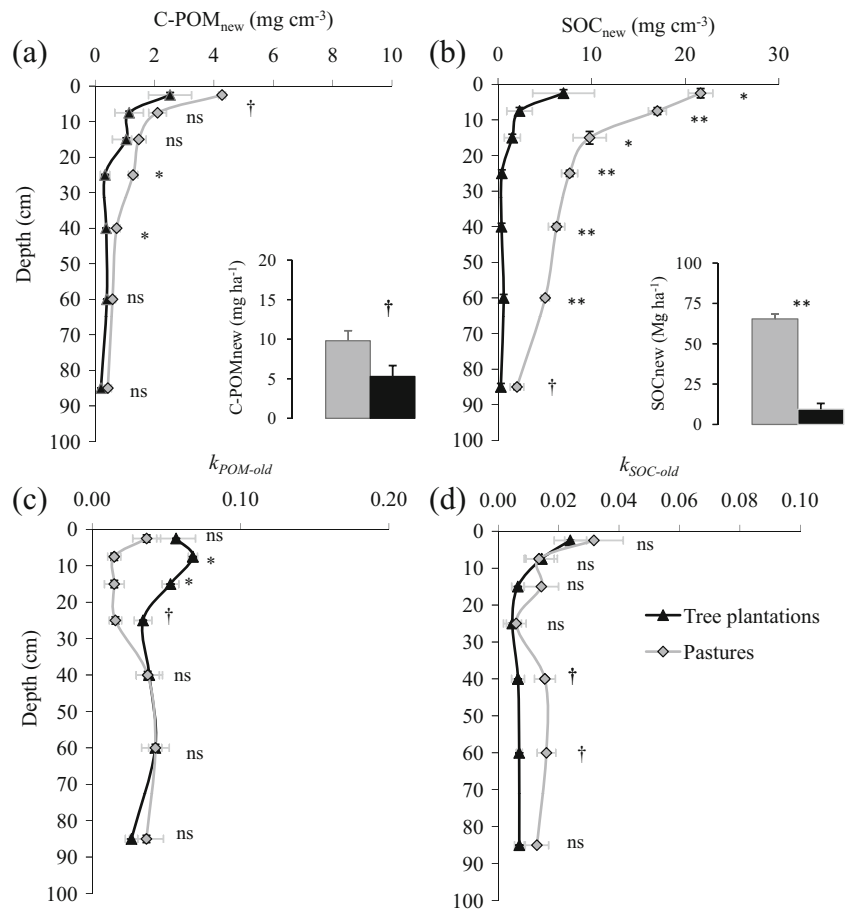
SOC changes in both land use transitions were mainly explained by changes in the new carbon incorporated into the soil (SOC_{new}), while differences in outputs or decomposition rates ($k_{\text{SOC-old}}$) between land uses were less important (Fig. 4). The decomposition rates of the whole SOC pool ($k_{\text{SOC-old}}$), estimated from changes in $\delta^{13}\text{C}$ were similar between pastures and plantations in the topsoil, although they replaced different natural vegetation (forest or grassland). Therefore, observed SOC gains in the surface soil under pastures and SOC losses under tree plantations were both explained by changes in the new stabilized soil C derived from the cultivated vegetation (SOC_{new}). Pastures incorporated large amounts of SOC_{new} (and also $\text{C-POM}_{\text{new}}$) that maintained high SOC levels while tree plantations incorporated only scarce

amounts of SOC_{new} , generating decreases in total SOC stocks (Fig. 4). Only in deep soil layers and under pastures, SOC losses can be attributed to increases in decomposition (higher $k_{\text{SOC-old}}$ values) (Fig. 4d). Overall, pastures incorporated 65.4 Mg ha⁻¹ of SOC_{new} and tree plantations only 9.4 Mg ha⁻¹ for the whole soil profile studied. POM changes followed similar patterns, but were less important in magnitude (Fig. 4).

The chronosequence of replacements to pastures or tree plantations showed how the amounts of SOC_{old} , $\text{C-POM}_{\text{old}}$, SOC_{new} and $\text{C-POM}_{\text{new}}$ changed with time, supporting patterns described previously based on the vertical soil profiles. SOC_{old} decreased faster under pastures than tree plantations (because its higher $k_{\text{SOC-old}}$), but pastures maintained similar SOC levels in time by storing large amounts of SOC_{new} that refilled SOC_{old} losses. On the other hand, tree plantations decreased total SOC stocks in time due to their low incorporation of SOC_{new} , although they showed small decreases in SOC_{old} (Fig. 5). Similar trends were observed in the POM fraction (Fig. 5).

When the two land uses were considered together, changes in total SOC and C-POM contents were associated with changes in SOC_{new} and $\text{C-POM}_{\text{new}}$, respectively, but not to their respective outputs constants ($k_{\text{SOC-old}}$ and $k_{\text{POM-old}}$) (Fig. 6). This result suggests a greater importance of C inputs rather than outputs determining overall net shifts in SOC and C-POM. These

Fig. 4 New carbon incorporated into particulate organic matter ($C\text{-}POM_{\text{new}}$, panel a) and SOC (SOC_{new} , panel b) and decomposition rates of old C in and POM ($k_{POM\text{old}}$, panel c) and SOC ($k_{SOC\text{old}}$, panel d) for pastures and tree plantations at different soil depths



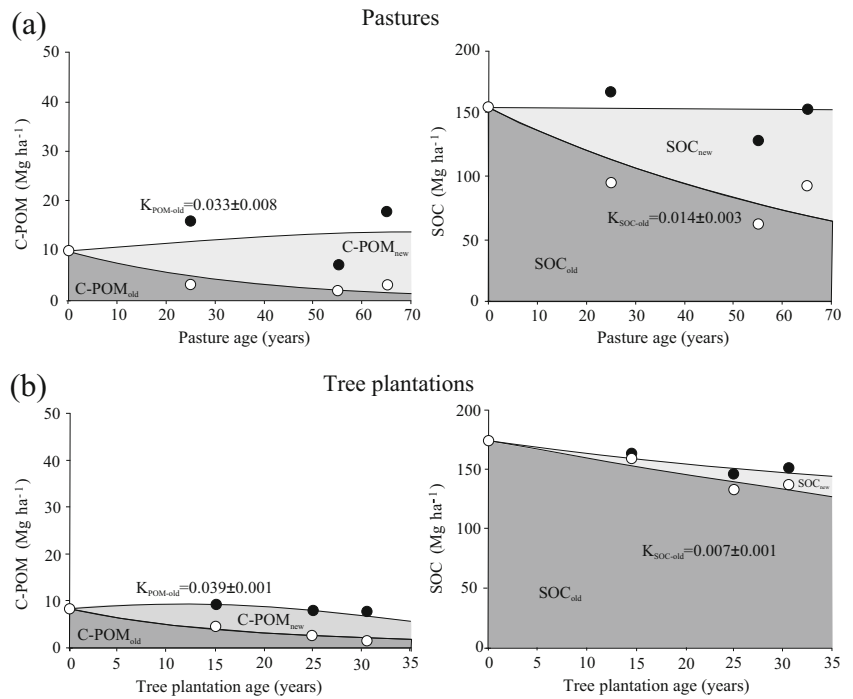
changes were coincident with the high BNPP of pastures and their high C:N ratios of pasture's litter and fine roots, compared to the native forests replaced (Tables 2 and 3). On the other hand, tree plantations reduced total BNPP as compared to grasslands, although they increased ANPP and total NPP. The low estimated BNPP of tree plantations (in spite of their higher NPP) could explain their low incorporation of SOC_{new} leading to SOC losses.

Discussion

Carbon inputs shifts and their stabilization in the soil appear as the main drivers of SOC changes which occurred after the establishment of pastures and tree plantations over grasslands or native forests, respectively (Fig. 7). Although, it is well documented that increases in plant inputs have a positive effect on SOC levels (Kong et al. 2005; Rasmussen and Parton 1994),

several contributions stress the relevance of increased C outputs coming with cultivation and respiration as SOC change drivers (Alvarez and Alvarez 2000; Balesdent et al. 2000; Six et al. 1999). Remarkably, most of this work has been carried out in annual cropping systems where repeated plowing can stimulate decomposition rates. Perennial systems such as the ones we studied showed a very different picture, one in which the initial effects of plowing and soil preparation were likely diluted over time (Cerri et al. 1991; Chonè et al. 1991; Freier et al. 2010), giving a preponderant role to the behavior of C inputs afterwards. In accordance, Iqbal et al. (2009) found higher SOC decomposition rates in annual cropping systems than in tree plantations, yet Raich and Tufekcioglu (2000) found no differences. Our results confirm that soil C inputs derived from the new landuse are key drivers of SOC levels under perennial systems, and encourage future work on no-till cropping systems, where plowing is absent (Mazzilli et al. 2014). However, our results also showed that C

Fig. 5 Changes through time in SOC_{old} and $C-POM_{old}$ remaining from forest and grasslands and SOC_{new} and $C-POM_{new}$ derived from (a) pastures and (b) tree plantations. Equations were fitted using least square adjustments with exponential decay models for $C-POM_{old}$ and SOC_{old} , while equations for $C-POM_{new}$ and SOC_{new} were adjusted using quadratic or exponential models with SigmaPlot software



decomposition rates can be driving SOC losses in deep soil layers under pastures, but this result can also be attributed to higher C inputs to deeper layers (see higher

SOC_{new} in Fig. 4) that may have increased decomposition rates ($k_{SOC-oldest}$) by a priming effect already reported in other ecosystems (Mazzilli et al. 2014).

Fig. 6 Relationships between (a-b) C inputs to the soil ($C-POM_{new}$ and SOC_{new}) and (c-d) C outputs from the soil ($k_{POM-oldest}$ and $k_{SOC-oldest}$) with SOC and C-POM changes on 100 cm soil depth, occurred after the replacement of natural vegetation with plantations or pastures. Each number in the graphs represents a different site; see Table 1 for sites names and description

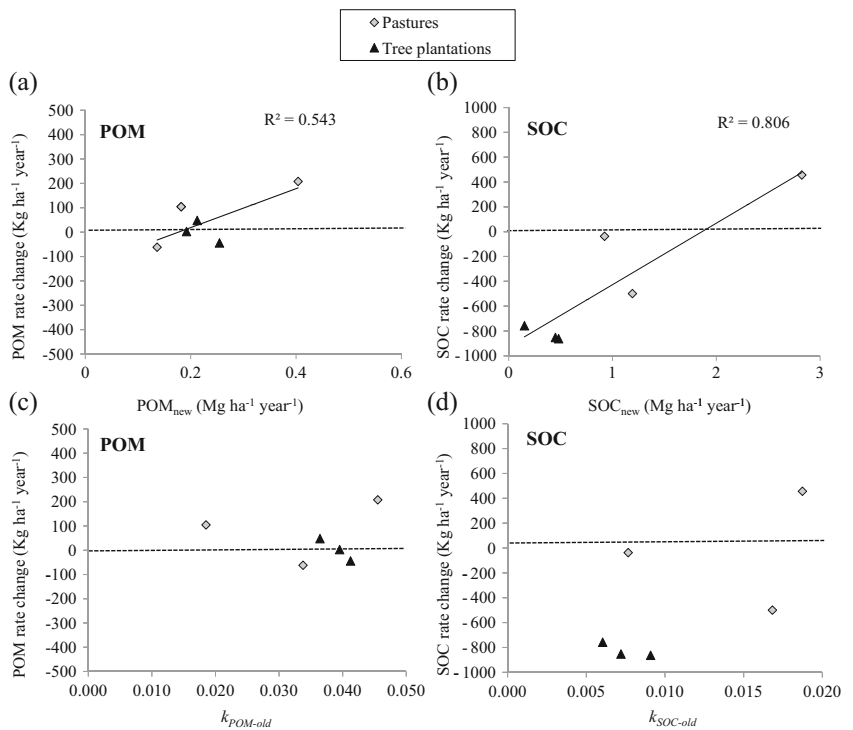


Table 3 C:N ratios of litter and fine roots before and after the conversion of forests to pastures and grasslands to tree plantations

Site	Land use transition ^a	C:N Initial land use				C:N Current land use				C:N Differences ^b			
		SOC	POM	Litter	Fine root	SOC	POM	Litter	Fine root	SOC	POM	Litter	Fine root
1	F-P	9.0	16.8	16.3	26.3	10.3	21.4	32.6	61.0	14.4	27.5	99.6	130.1
2	F-P	9.0	16.8	16.3	26.3	10.6	23.3	25.1	68.5	17.4	38.9	53.4	159.8
3	F-P	10.8	20.2	22.8	47.7	10.5	20.9	34.9	74.4	-1.2	3.6	52.8	55.8
4	G-T	12.6	21.1	42.5	76.3	12.7	22.4	62.1	78.6	1.1	5.8	46.0	3.0
5	G-T	12.1	35.9	40.0	120.2	12.2	31.4	49.2	70.4	1.0	-12.5	22.9	-41.5
6	G-T	12.7	24.9	46.2	120.8	12.1	23.4	41.0	54.6	-4.4	-6.0	-11.4	-54.8
Means comparing the conversion to ^c :													
Pastures										10.2 a	23.3 a	68.6 *a	114.7 *a
Plantation										-0.77a	-4.2 a	19.2 a	-30.7 b

^a F forest, G grassland, P pasture, T tree plantation

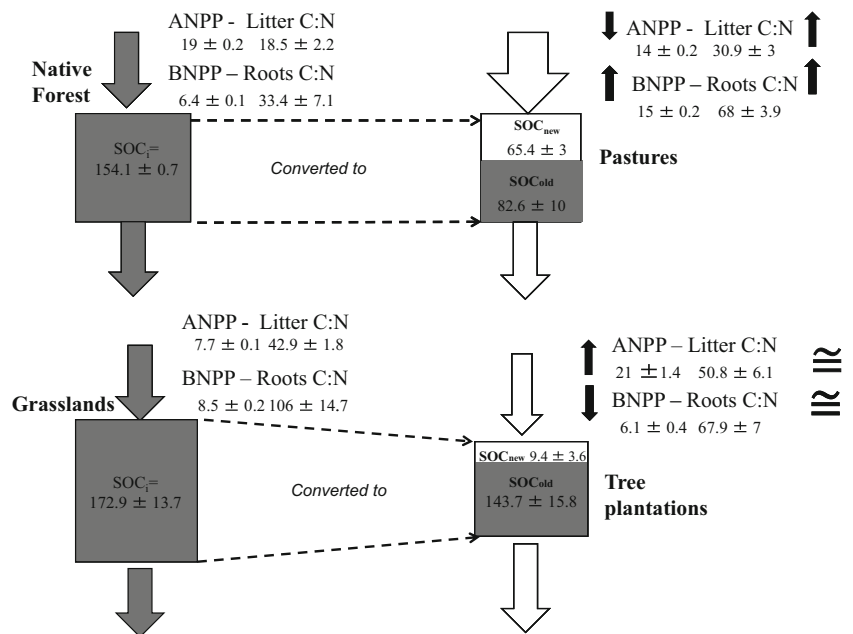
^b Changes are expressed as % of initial C:N

^c Different letters within a column indicate significant differences at $p < 0.05$ between pastures and plantations and the asterisks indicate a significant change after conversion to pasture or to tree plantation ($* = p < 0.05$)

Likely, plantations delayed the formation of SOC_{new} after their establishment as a result of their retention and high allocation of C into woody components (Fig. 5). As expected SOC_{new} increased as plantations and pastures aged, while SOC_{old} decreased. However, in plantations SOC_{new} was lacking during the first years after establishment and only increased slightly in older plantations.

Some studies have reported that in young tree plantations, a large portion of NPP ends in wood (30–40 %) (Litton et al. 2007; Ryan et al. 2004) and therefore does not reach the ground for a long time. Despite this, in older tree plantations C accumulation in standing biomass may cease and a higher proportion of NPP can eventually reach the soil (via dead leaves, trunks and

Fig. 7 Schematic representation of all changes occurred after replacing forests with pastures and grasslands with tree plantations. Pastures maintained SOC contents mainly by increasing C inputs to the soil and hence SOC_{new}, and also increased BNPP and C:N ratios of plant inputs. On the other hand, plantations decreased SOC contents mainly by decreasing C inputs to the soil and hence SOC_{new}, while increasing ANPP but decreasing BNPP and maintaining similar C:N ratios of plant inputs



roots) increasing C inputs to the soil and SOC stocks (Eclesia et al. 2012; Freier et al. 2010).

Our results showed that SOC decomposition rates ($k_{SOC-old}$) of the old organic matter derived from the native vegetation did not differ after planting trees or sowing pastures in the topsoil. It has been previously noticed that forests and grasslands present different soil respiration rates even when growing under similar conditions (Raich and Tufekcioglu 2000), which is why the similarity between $k_{SOC-old}$ in our study was unexpected, particularly given that decomposition took place under the contrasting soil environments hosted by pastures and tree plantations. However, these and other authors have pointed out that SOC decomposition rates are mainly determined by soil physical and mineral properties exerting a protective influence on C stocks and their access by microbes (Amundson 2001; Dungait et al. 2012; Epstein et al. 2002). Soils with high percentages of clay and oxides show usually an elevated protection of SOC, which determines low decomposition rates (Wattel-Koekkoek et al. 2003; Zinn et al. 2007). All our study sites had similar soils, with approximately 90 % of total SOC associated to the mineral soil fraction (Table 1), and therefore soil properties could be defining surface soil decomposition rates and overwhelming vegetation effects. On the other hand,

Our results also highlights the importance BNPP with SOC storage, which is in agreement with other works (Balesdent and Balabane 1996; Bird et al. 2008; Bird and Torn 2006; Mazzilli et al. 2015). Although

NPP represents the maximum amount of C that will eventually reach the soil, a large proportion of ANPP can be consumed by herbivores or stored in above-ground organs, decreasing the energy flux to decomposers (Chapin et al. 2002). Therefore, pastures may increase C inputs to the soil because of their elevated BNPP, and particularly their elevated production of fine roots that can be up to 4 times higher than in forest (Trumbore et al. 2006). Tree plantations, on the other hand, allocate less NPP to BNPP, and less BNPP to fine roots, decreasing SOC formation. In a global review, Liao et al. (2010) observed that in forest-to-plantation transitions fine-root biomass decreased 66 %, whereas Cuevas et al. (1991) observed a 35 % reduction. Moreover, management strategies aimed to increase BNPP in either plantations or pastures could be a promising way of increasing SOC stocks.

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Appendix

Table 4 List of abbreviations

Abbreviations	Description
SOC	Total soil organic Carbon
SOC _i	Initial amount of SOC in native ecosystems
SOC _e	Final amount of SOC in modified ecosystems
SOC _{new}	New SOC derived from plantations or pastures
SOC _{old}	Amount of old SOC derived from the native vegetation
fSOC _{old-remaining}	Proportion of old SOC remaining compared to SOC _i
C-POM	C in the particulate soil organic matter fraction
C-POM _i	Initial amount of C-POM in native ecosystems
C-POM _e	Final amount of C-POM in modified ecosystems
C-POM _{new}	New C-POM derived from plantations or pastures
C-POM _{old}	Amount of old C-POM derived from the native vegetation
fC-POM _{old-remaining}	Proportion of old C-POM remaining compared to C-POM _i

Table 4 (continued)

Abbreviations	Description
fC-POM _{new}	Proportion of new C-POM compared to C-POM _i
<i>t</i>	Age or time elapsed since de replacement of native vegetation (years)
δ _e	Final value of δ ¹³ C of the SOC (or C-POM) in pastures or plantations
δ _i	Initial value of δ ¹³ C of the SOC (or C-POM) in native ecosystems
δ _v	δ ¹³ C of new plant (pastures or plantations) inputs to soil
<i>k</i> _{SOC-old}	Decomposition rate of old SOC (derived from native vegetation)
<i>k</i> _{POM-old}	Decomposition rate of old C-POM (derived from native vegetation)
NPP	Net primary production
BNPP	Belowground net primary production
ANPP	Aboveground net primary production

Table 5 Estimates of productivity from radiation interception and vegetation indexes measured by MODIS satellites, at sites with natural vegetation (forest and grasslands) and pastures or tree plantations

Site	Ecosystems ^a	NDVI	fPAR ^b	ε ^c	ANPP	BNPP/ANPP ratio ^d	BNPP	NPP
1	F	0.86	0.84	0.85	19.50	0.33	6.44	25.94
	P	0.77	0.71	0.73	14.34	1.1	15.77	30.11
2	F	0.86	0.84	0.85	19.50	0.33	6.44	25.94
	P	0.76	0.71	0.73	14.21	1.1	15.63	29.84
3	F	0.84	0.8	0.85	18.78	0.33	6.20	24.98
	P	0.74	0.68	0.73	13.64	1.1	15.00	28.64
4	G	0.66	0.57	0.5	7.83	1.1	8.61	16.43
	T	0.72	0.65	1.2	20.88	0.29	6.06	26.94
5	G	0.67	0.58	0.5	7.87	1.1	8.66	16.52
	T	0.77	0.72	1.2	23.39	0.29	6.78	30.18
6	G	0.64	0.55	0.5	7.44	1.1	8.18	15.63
	T	0.66	0.58	1.2	18.61	0.29	5.40	24.01
Averages ^c	F	0.85 a	0.83 a		19.26 a		6.36 c	25.62 a
	G	0.66 c	0.57 c		7.71 c		8.48 b	16.19 b
	P	0.76 b	0.70 b		14.06 b		15.47 a	29.53 a
	T	0.72 bc	0.65 bc		20.96 a		6.08 c	27.04 a

^a F forest, G grassland, P pasture, T tree plantation

^b fPAR is the fraction of photosynthetically active radiation intercepted by green tissues, BNPP = belowground net primary productivity, ANPP = aboveground net primary productivity and NPP = net primary productivity. BNPP, ANPP and NPP are expressed in Mg of biomass ha⁻¹ year⁻¹, NDVI is dimensional less, fPAR is in % and ε is in g of biomass. MJ⁻¹

^c ε = coefficient of conversion of absorbed radiation into biomass, efficiencies for each type of vegetation were obtained from (Ruimy et al. 1994; Turner et al. 2006; Yadvinder et al. 2009)

^d BNPP/ANPP ratios were derived from (Paruelo et al. 2010; Ruimy et al. 1994; Yadvinder et al. 2009)

^e Different letters within a column indicate significant differences $p < 0,05$

Plant production values estimated from remote sensing in our work were similar than those measured by other studies. NPP of subtropical grasslands varies from 6 to

16 Mg ha⁻¹ year⁻¹ (Gomez and Gallopin 1991; Grace et al. 2006; Sundaravalli and Paliwal 2000), while forest NPP varies between 20 and 25 Mg ha⁻¹ year⁻¹ (Grace

et al. 2006; Ito and Oikawa 2004; Malhi et al. 2009), although in a global review Clark et al. (2001) observed extreme values between 3.4 to 43.4 Mg ha⁻¹ year⁻¹. On the other hand in plantations, NPP of *Pinus elliotti* and *P. taeda* in other regions are between 10 and 20 Mg ha⁻¹ year⁻¹ (Clark et al. 2001; Grace et al. 2006; Ito and Oikawa 2004; Litton et al. 2007), but ANPP in similar sites of the province of Misiones was reported around 34.8 ± 1.5 Mg ha⁻¹ year⁻¹ (Pérez et al. 2006); while NPP measurements of tropical pastures are between 28 and 40 Mg ha⁻¹ year⁻¹ (Boddey et al. 2004; Fisher et al. 1997; Rezende et al. 1999)

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